

Articles

THE DYNAMIC LANDSCAPE : PERTURBATION, BIOTIC RESPONSE, BIOTIC PATTERNS

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INTRODUCTION

Much of ecological theory was developed under two assumptions: (1) that the environment is relatively stable and consequently, (2) biotic populations or communities maintain homeostasis except during irregular periods of catastrophic perturbation. These assumptions have dominated ecological thinking at most organizational levels. For example, each of the following hypotheses has a large group of supporters. *Environmental stability results in community structure being determined primarily by endogenous agents such as competition (Diamond 1975). *In each climatic region, vegetation reaches an equilibrium state where species replace themselves (Clements 1936). *Environmental change on the evolutionary time scale is gradual such that rates of speciation and extinction are constant (Marr 1970). The simplifying assumptions of environmental stability and biotic equilibrium have been very useful, perhaps even necessary, in initial attempts to understand complex natural systems.

More recently, however, 'second generation' theory has permeated ecological thinking. The failure of some equilibrium theory to withstand empirical testing and increasing paleoecological data showing the pervasiveness of change (eg Delcourt and Delcourt 1983) encouraged the development of 'disequilibrium' theory. This approach concentrates on the effects of environmental heterogeneity. Hypotheses derived from disequilibrium theory include those listed below. *Ecological change sometimes outpaces evolutionary change such that some modern traits in organisms are anachronisms (Janzen and Martin 1982). *Natural disturbance disrupts ecological communities so frequently that the role of competition in structuring communities is minor (Connell 1978). *Climate is continually changing so vegetative climax is not reached (Bodkin and Sobel 1975). *Long term environmental change is abrupt rather than continuous such that periods of speciation and extinction are episodic (Stanley 1979).

Most ecologists would agree that this recent emphasis on environmental dynamics complements and balances equilibrium theory. Surprisingly, though, only recently has there been much effort to develop a general theory of the consequences of environmental dynamics on the biota (ie Mooney et al 1983, Pickett and White 1984). A great deal remains to be done. Many scientists have examined the effects of specific types of disturbance on organisms but no definition of disturbance is widely accepted. A general framework for classifying and quantifying perturbations has not yet been fully developed. Finally, little work has been done on the general types of biotic responses to environmental variation.

In this paper we present some initial ideas on a conceptual model that links perturbations, resource dynamics, biotic responses, and biotic patterns. Further, we briefly discuss some implications of the model for ecologists. The goal of our research is to develop the model in more detail and to test hypotheses derived from it with field data. To that end, we conclude with a request for empirical information of environmental dynamics and the responses of plants and animals in Southern Africa.

A LANDSCAPE PARADIGM

Factors Constraining Life

The status of any living thing is largely determined by its success in obtaining and processing resources. Thus, life is limited either by resource shortages or by agents which disrupt or destroy the physiological mechanisms for processing resources (ie predation, disease, injury). The situation is commonly illustrated in introductory ecology texts as a graph of the size of a population over time. The population is shown to increase until environmental constraints halt growth at carrying capacity. The ultimate environmental constraints are often resource shortages and physiological disruptors. Consequently, in the quest to examine the effects of environmental dynamics on the biota, the type of variation of interest is in resources and physiological disruptors. From here on we refer to change in these two factors as environmental variation.

The Basic Scheme

A conceptual model of the origins of environmental variation and its consequences to life is presented in Figure 1. In the model, perturbations alter resources or act as physiological disruptors such that responses are elicited

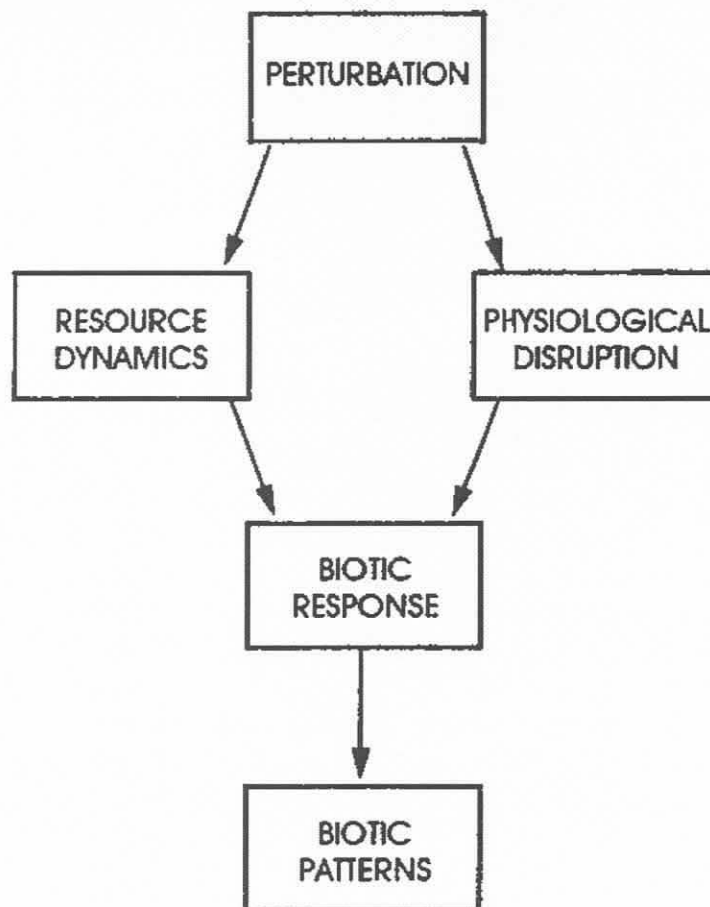


FIG. 1 Conceptual model of the components of landscape dynamics

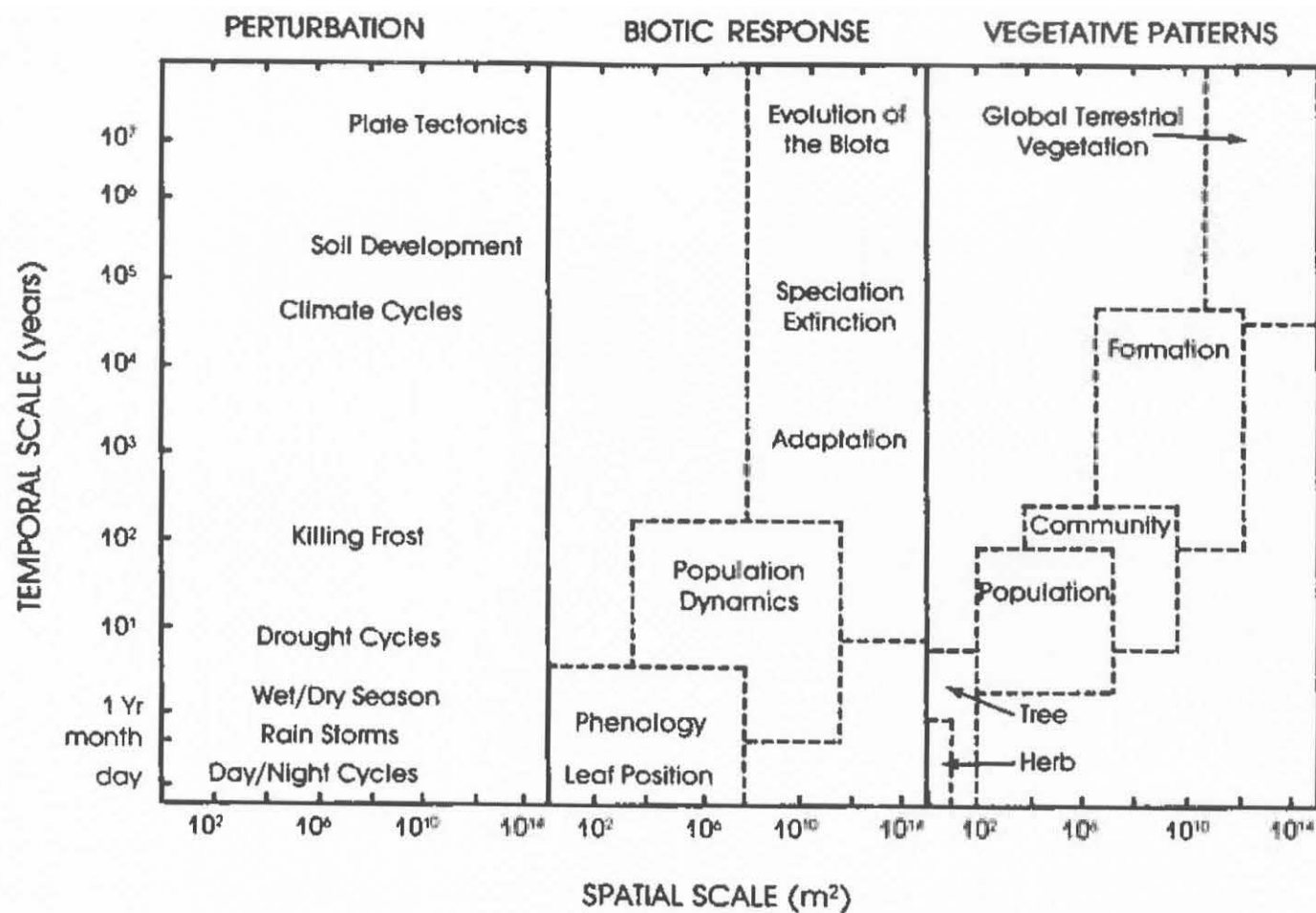


FIG. 2

Environmental perturbation regimes, biotic responses and vegetative patterns viewed in a hierarchy of space-time domains. The time scale for each process or pattern reflects the sampling intervals required to observe it. (Modified from Delcourt, Delcourt and Webb 1983).

from the biota. Possible responses in plants range from adjusting stomata size, to changes in population numbers, to shifts in the plant biomass in an ecosystem. These responses, in turn, determine the biotic patterning across the landscape. For example, rainfall is an important determinant of soil moisture available to plants. An unusually dry period may result in plant species either flourishing or dying depending upon their soil moisture tolerances. The drought and the responses of plants then determine the patterns of species abundance across the landscape. An example of disturbance that influences plants through physiological disruption is frost. It may destroy tissue and thus inhibit the processing of resources.

Hierarchical Nature of the Scheme

The relationships between perturbation, biotic response and biotic pattern are fundamentally hierarchical (Fig 2). Perturbations range in scale from those occurring in seconds and influencing an area of a few square centimeters (ie a hoof print) to episodes of continental drift which may span hundreds of millions of years. The dynamics of resources, responses of the biota and the resulting biotic patterns all occur on a scale that corresponds with the scale of the perturbation. For example, variation in soil moisture in southern Africa probably occurs at several scales with periodicities ranging from a month to 10 000 years (Fig 3). A specific perturbation is responsible for each of the spectral peaks (recurrence intervals of characteristic variation) and biotic responses are elicited by each peak.

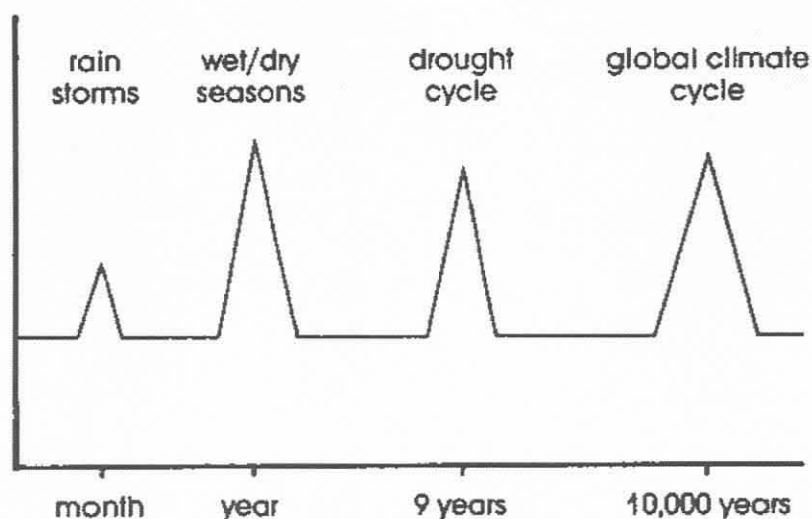


FIG. 3 Hypothetical spectral analysis of variation in soil moisture in southern Africa as a function of precipitation. The vertical axis denotes degree of correlation. Each peak shows a region of characteristic variation.

Monthly rainfall events might stimulate increased productivity in plants in a watershed while nine-year drought cycles might influence population dynamics and thus determine species composition in herbaceous vegetation throughout a region. Long-term climatic variation might facilitate plant speciation and extinction.

An implicit assumption in Figure 2 is that a perturbation is felt primarily by those elements in the biota that are of similar scale. This assumption is derived from the recent formalization of a theory of hierarchy by Allen and Starr (1982). They consider many ecological systems to be comprised of nested

levels called holons (ie tree, forest, landscape). Each holon has a characteristic time/space domain; moving up the hierarchy, successive levels generally behave more slowly but cover a larger area. Each level has unique properties which integrate into emergent properties at the next level up. Attributes of individual trees (growth rate, reproduction, survival) collectively merge to define the intrinsic rate of increase at the population level. Information is filtered as it passes between holons such that events at one level may be inconsequential several levels up. This filtering phenomenon is the basis of the assumption that perturbations are only felt by biotic entities of corresponding scale. A small and ephemeral event, for example, passes unnoticed at higher levels. The death of a single tree in a forest is a case in point. Similarly, a large and long-lived perturbation may not influence an entity of lesser scale if that entity exists between pulses of the perturbation. Periodic ice ages are of no consequence to the survival of people alive today. Interestingly, if perturbation and biotic entity are very similar in scale, the entity may, over time, adapt or habituate such that the perturbation is necessary to maintain equilibrium. Fire in some savanna systems does not disrupt community composition; it maintains it. The important implication here is that a perturbation may have very different effects upon different elements of the biota and consequently, it can only be classified relative to specific biotic entities.

Classification of Perturbations

The type of perturbation most closely examined in recent studies of environmental heterogeneity is disturbance. However, no definition of disturbance has been generally accepted. Menges and Loucks (1984) suggest disturbance is an episodic phenomenon leading to unusually high mortality in some segment of the community. White (1979) sees disturbance as an agent that results in structural changes in plant communities that usually involve the death of plant parts. While Bazzaz (1983) defines it as a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response. These authors and perhaps most ecologists view disturbance as an irregular event that forces populations or communities away from a near equilibrium condition. However, the elements not yet resolved are: (1) what constitutes an 'irregular' event; (2) the mechanisms by which disturbance affects the biota; (3) the hierarchical level at which the effects are felt by the biota; and (4) the position of the boundary between dynamic equilibrium and disequilibrium. Also unresolved is the treatment of perturbations that are not disturbance.

We suggest that the primary agents of environmental variation are of three fundamental types: disturbance, incorporated disturbance, and non-events (see also Allen and Starr 1982). The main suppositions of our classification scheme are that: the hierarchical nature of ecological systems requires that a perturbation be classified relative to specific entities; perturbations influence the biota via resources or directly by disrupting physiological processes; the regularity of a perturbation need be measured relative to the conditions to which the entity is adapted; and there is generally no discrete boundary between equilibrium and disequilibrium. The three possible effects a perturbation may have on a biotic entity are (Fig 4):

1. The event may alter the dynamics of limiting resources or disrupt physiological processes such that the entity is forced into a new state. (DISTURBANCE).
2. The event may elicit dynamics of a scale to which the entity is adapted and thus be necessary to maintain the entity in its present state. (INCORPORATED DISTURBANCE)
3. The event may either not alter the functional environment of the entity or it may do so but with a frequency or intensity too minor to elicit a response. (NON-EVENT)

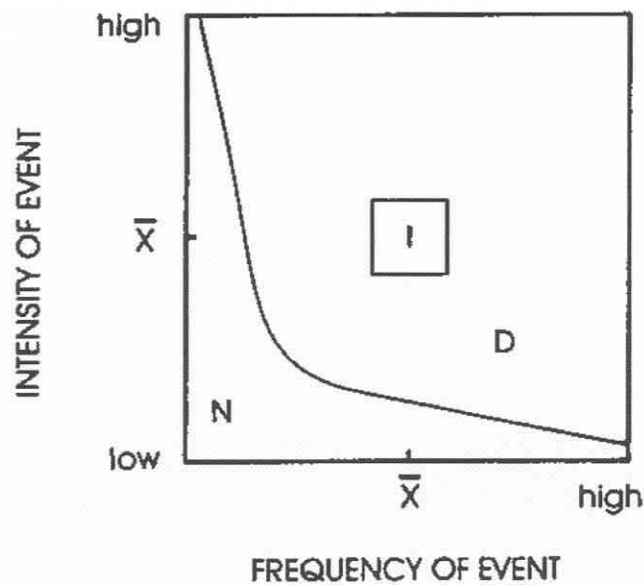


FIG. 4 Regions of state space where perturbations are INCORPORATED DISTURBANCE (I), DISTURBANCE (D), or NON-EVENTS (N) relative to a specific biotic entity. The axes denote the mean and range of intensity and frequency of perturbation experienced by the entity.

It is imperative to point out that these three categories are not separated by discrete borders. Rather they represent extremes in a three way continuum. Their value is to aid in conceptualizing the possible effects of perturbation. Actually implementing this scheme in an empirical world will often require a fairly arbitrary decision as to what constitutes a change of state in an entity.

The Landscape Perspective

The relationships between perturbation, resource dynamics and biotic response can perhaps best be visualized from a landscape perspective. A landscape is seldom homogenous, rather it is a dynamic mosaic of patches each containing a specific regime of perturbation, resource dynamics, and biota (Watt 1947, Shutgart 1984). Figure 5 illustrates that spatial patchiness in plant biomass results from differential soil moisture across the landscape which is itself a consequence of patchy rainfall. Of course, the dimensions of the patches in reality vary greatly in size such that a landscape is actually a complex of patches of differing spatial scale which overlay one another (Fig 6). The patches are also dynamic through time. Typically the larger patches change more slowly and may seem static relative to the fast turnover times of smaller patches.

IMPLICATIONS

This conceptual model of environmental dynamics appears to have important implications for ecologists. First, it is clear that we should ask not if natural systems change, but rather how fast they change and what are the ramifications of this change for the problem of interest. Secondly, the model suggests that problems should be approached on the appropriate level. To understand the factors controlling the population dynamics of savanna trees, it is probably necessary to consider events with periodicities of tens to hundreds of years over regional areas. For example, bush encroachment in southern Africa may be partially a result of long-term climate change which favours woody plants. We are somewhat constrained by our own characteristic scale but can overcome this problem through use of tools which allow us to jump down-scale (ie microscopes, radioactive tracers) or up-scale (ie analysis of fossil pollen or bones,

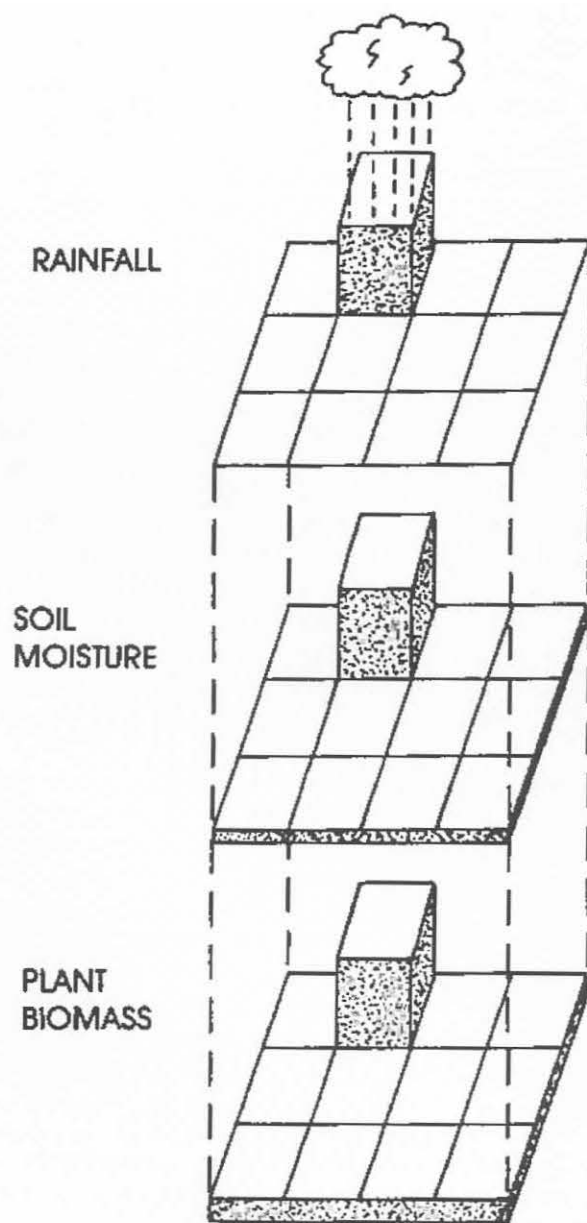


FIG. 5

Representation of the relationships between perturbation, resources, and biotic response across a spatial landscape. In reality the three factors are superimposed on one plane.

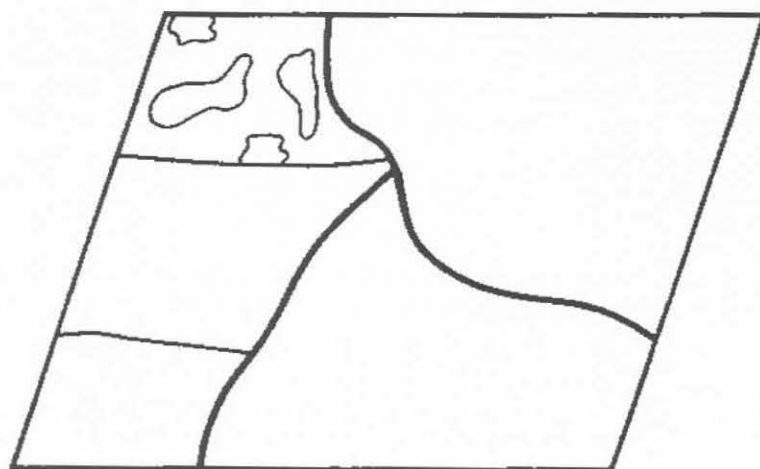


FIG. 6

A landscape is composed of patches of differing scale that overlay one another.

satellite images, simulation models). Third, we need to be cognizant of the fact that a given perturbation elicits different responses from organisms of different scale. The recent drought in southern Africa caused radical change in species composition of grasses in some areas but had little effect on tree composition (R J Scholes, R Emslie personal communication). Finally, many types of human disturbance probably have a much greater effect on the biota than natural disturbance of similar scale. Human perturbations are often without historical precedence and thus the biota has not had time to adapt to them. Consequently, anthropogenic disturbance may elicit radical responses.

CALL FOR DATA

We wish to test hypotheses derived from the landscape model with field data from savannas of southern Africa. Long-term records of perturbation regimes or the subsequent responses of plants and animals appear to be sparse. Thus we would appreciate hearing from anyone with knowledge of such information. Ideal data sets would be sufficiently quantitative to allow for parameterization of perturbation and resource dynamics according to Tables 1 and 2. Of course, we are also interested in hearing of less rigorous data sets.

TABLE 1	Parameters characterizing perturbation
FREQUENCY	number of occurrences per unit time
SIZE	area over which the event occurs
INTENSITY	degree to which the event influences the biota relative to the maximal response elicited by a perturbation within the specified hierarchical scale
DURATION	length in time of each occurrence
TIMING	time of year or phenological stage at which the event occurs
PATTERNING	degree of synchrony of perturbation in quadrats of specified region
LIFESPAN	length of time the perturbation regime has been in existence
SELECTIVITY	proportion of the biota of appropriate scale that is influenced by the perturbation
MECHANISMS	whether the event alters resources, directly effects the biota, or both
VARIABILITY	probability functions or standard deviations for each of the above

TABLE 2	The parameters characterizing resource dynamics
FREQUENCY	wave length of cycle
SIZE	area over which the dynamics regime is consistent
LEVEL	abundance of resource in absolute units (ie degrees C)
DURATION	length of time resource level is away from the mean value
TIMING	actual time when changes of interest occur
PATTERNING	synchrony of resource change in quadrats within a region
LIFESPAN	length of time the resource regime has existed
PERIODICITY	position of spectral peaks
VARIABILITY	probability functions or standard deviations of the above

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